PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
116(1):1–15. 2003.

Cranial variation in Columbian white-tailed deer populations: implications for taxonomy and restoration

Winston P. Smith, Leslie N. Carraway, and Thomas A. Gavin

(WPS) U.S. Forest Service, Pacific Northwest Research Station, Forestry Sciences Laboratory, 2770 Sherwood Lane—Suite 2A, Juneau, Alaska 99801-8545, U.S.A., e-mail: Winston_Smith@fs.fed.us;
(LNC) Department of Fisheries and Wildlife, Nash 104, Oregon State University, Corvallis, Oregon 97331-3803, U.S.A., e-mail: carver@proaxis.com;
(TAG) Department of Natural Resources, Cornell University, Ithaca, New York 14853-2801, U.S.A., e-mail: tag1@cornell.edu

Abstract.—We examined variation in 18 cranial dimensions among three disjunct populations of white-tailed deer (*Odocoileus virginianus*) in the Pacific Northwest to test the hypothesis that they represent a single taxon. Previous allozyme analyses indicated considerable variation among the three populations, but genetic divergences were less than conventional benchmarks used to distinguish subspecies. We observed substantial variation in cranial dimensions among the three populations that graphically sorted into three distinct morphological groups and corresponded with east-west and north-south geographical gradients. Specimens of the northwestern white-tailed deer (*O. v. ochrourus*) from northern Idaho had longer and broader skulls than did Columbian white-tailed deer (*O. v. leucurus*) from the lower Columbia River or southwestern Oregon; specimens from southwestern Oregon had shorter rostra and narrower crania than those from the lower Columbia River. Even after controlling for differences in size related to age or sex, specimens from southwestern Oregon were relatively smaller animals with shorter faces and narrower posterior portions of the skulls than specimens in the other populations. These results do not support the hypothesis that the three groups represent a single taxon, nor do the results support the current taxonomy. Sample sizes were insufficient to fully evaluate if designating the three populations as distinct subspecies is warranted. Still, the three populations show considerable morphological and genetic variation, remain disjunct and isolated from each other, and likely are evolving along different trajectories because of geographical variation in habitat.

The Columbian white-tailed deer (*Odocoileus virginianus leucurus* [Douglas, 1829]) is one of three currently recognized subspecies of *Odocoileus virginianus* (Zimmermann 1780) indigenous to the western United States (Smith 1991). Historically, Columbian white-tailed deer (CWTD) occurred throughout most of western Oregon and southwestern Washington lowlands, associated with riparian vegetation of broad river valleys (Douglas 1829, Smith 1985). Extensive development of western Oregon following European settlement led to extirpation of CWTD from most of its historic range, including the Willamette Valley of west-central Oregon (Smith 1985). Jewett (1914) and Bailey (1936) concluded that CWTD survived in the Willamette Valley until late in the 19th century. Today, its distribution is limited to two isolated popula-

Fig. 1. Historic (stippled areas) and current (open circles and cross-hatching) distributions of Columbian white-tailed deer, *Odocoileus virginianus leucurus* Douglas (Smith 1985, 1987), and current distribution of Northwestern white-tailed deer, *O. v. ochrourus* Bailey, in Oregon and Washington (Johnson and Cassidy 1997, Washington Department of Fish and Wildlife 2000, Oregon Department of Fish and Wildlife, unpubl. data). Note that the Umpqua River branches into the North and South Umpqua rivers.

tions: one along the lower Columbia River composed of several subpopulations that occur on several islands upriver from a Washington mainland subpopulation; and a second in the interior valleys of the Umpqua River in Douglas Co., Oregon (Fig. 1). The CWTD remains allopatric with the other two western subspecies; the nearest, northwestern white-tailed deer (*O. v. ochrourus* Bailey 1932), is about 300 km east of the current range of *O. v. leucurus* (see Smith 1985, 1991).

The limited distribution of CWTD and imminent threat to remaining habitat prompted the U.S. Department of the Interior, Fish and Wildlife Service (FWS) to list *O. v. leucurus* as endangered in 1967 in the Federal Register (32 FR 4001). The Columbian White-tailed Deer National Wildlife Refuge (CWTDNWR) was established in 1972 and the Douglas Co. population was included in the listing in 1978 (Smith 1985). Since then, much effort has been expended toward recovery of the endangered populations, but the process has been slow and arduous (Doremus and Pagel 2001). The FWS developed a recovery plan with specific goals and measurable objectives, including information needs, to help the CWTDNWR and Douglas Co. populations recover (Columbian White-tailed Deer Recovery Team 1983). Numerous studies documented the status and provide information on the population ecology of CWTD (Gavin 1979, Suring & Vohs 1979, Dublin 1980, Gavin et al. 1984, Smith 1985, 1987; Ricca 2000, Whitney 2001), but little attention was given to the taxonomy or genetic in-

tegrity of CWTD populations (Gavin & May 1988).

The original taxonomic description of CWTD was based on specimens collected from near the mouth of the Columbia River and from the lower Willamette River [=falls at present-day Oregon City, Clackamas Co., OR] (Douglas 1829). Douglas (1914) reported CWTD throughout the central river bottomlands of western Oregon, perhaps as far south as the Umpqua River valleys (in what is now Douglas Co.). Crews (1939) extended the range south to Grants Pass, Josephine Co., Oregon. To our knowledge, however, the relationship between deer from Douglas Co. and deer from the region of the type locality was never rigorously examined. When Bailey (1932) described the northwestern white-tailed deer (*O. v. ochrourus*), he compared the type specimen to white-tailed deer collected by Jewett (1914) from Douglas Co. rather than to deer collected near the type locality of *O. v. leucurus*. Clearly, data supporting the original descriptions of these two taxa were limited.

Gavin & May (1988) evaluated the taxonomic status of CWTD by comparing allozymes from 35 loci among multiple populations of white-tailed deer representing three subspecies, including *O. v. ochrourus*. They concluded that genetic distance between the two CWTD populations and between each of the CWTD populations and populations of *O. v. ochrourus* in Washington and Oregon was less than the difference of two putative subspecies of widely separated geographic regions. Gavin & May (1988) did not observe a consistent pattern of differentiation at several loci; rather, their conclusions were based on variation at a single locus. Moreover, they recommended that an examination of additional evidence should occur before assigning subspecific status to any putative populations of CWTD. The purpose of this paper is to evaluate the taxonomy of *O. v. leucurus* by use of morphometric data. Our objectives were: 1) to quantitatively characterize crania of white-tailed deer from Douglas Co., Oregon, the CWTDNWR, and the historic range of northwestern white-tailed deer; 2) to determine if significant variation in cranial features exists among the three groups; 3) to compare findings of this morphological investigation to earlier findings based on genetic distance among the populations (Gavin & May 1988); and 4) to use the results of this study to test the working hypothesis that white-tailed deer in the three populations belong to a single taxon.

Materials and Methods

We examined crania of adult white-tailed deer from northern Idaho (n = 6 females, 12 males), the Columbian White-tailed Deer National Wildlife Refuge (CWTDNWR; Gavin & May 1988) in Washington and Oregon (n = 65 females, 52 males), and from Douglas Co., Oregon (n = 80 females, 49 males; Smith 1982). Samples from northern Idaho are museum specimens; age was determined by toothwear (Severinghaus 1949, Larson & Tabor 1980, Gee et al. 2002). Tom Gavin collected samples from the CWTDNWR (Gavin & May 1988); age was determined by number of tooth cementum annuli (Scheffer 1950). Samples from Douglas Co., Oregon, were collected by Winston Smith (1982); age was determined by either number of tooth cementum annuli or by toothwear (Larson & Taber 1980:154, Gee et al. 2002). Eighteen measurements (Fig. 2, Table 1) were recorded for complete crania. Many specimens were recovered dead along roads, and had damaged crania because of collisions with vehicles, which resulted in incomplete datasets for these animals. Gavin recorded all measurements. Because growth in deer does not become asymptotic until about 4 and 6 years-of-age for females and males, respectively, missing measurements were not estimated. We used data only from complete crania in statistical analyses.

Females were sorted into three age classes for each collection area: age class 1 contained 2–2.9 year olds, 2 contained 3–3.9

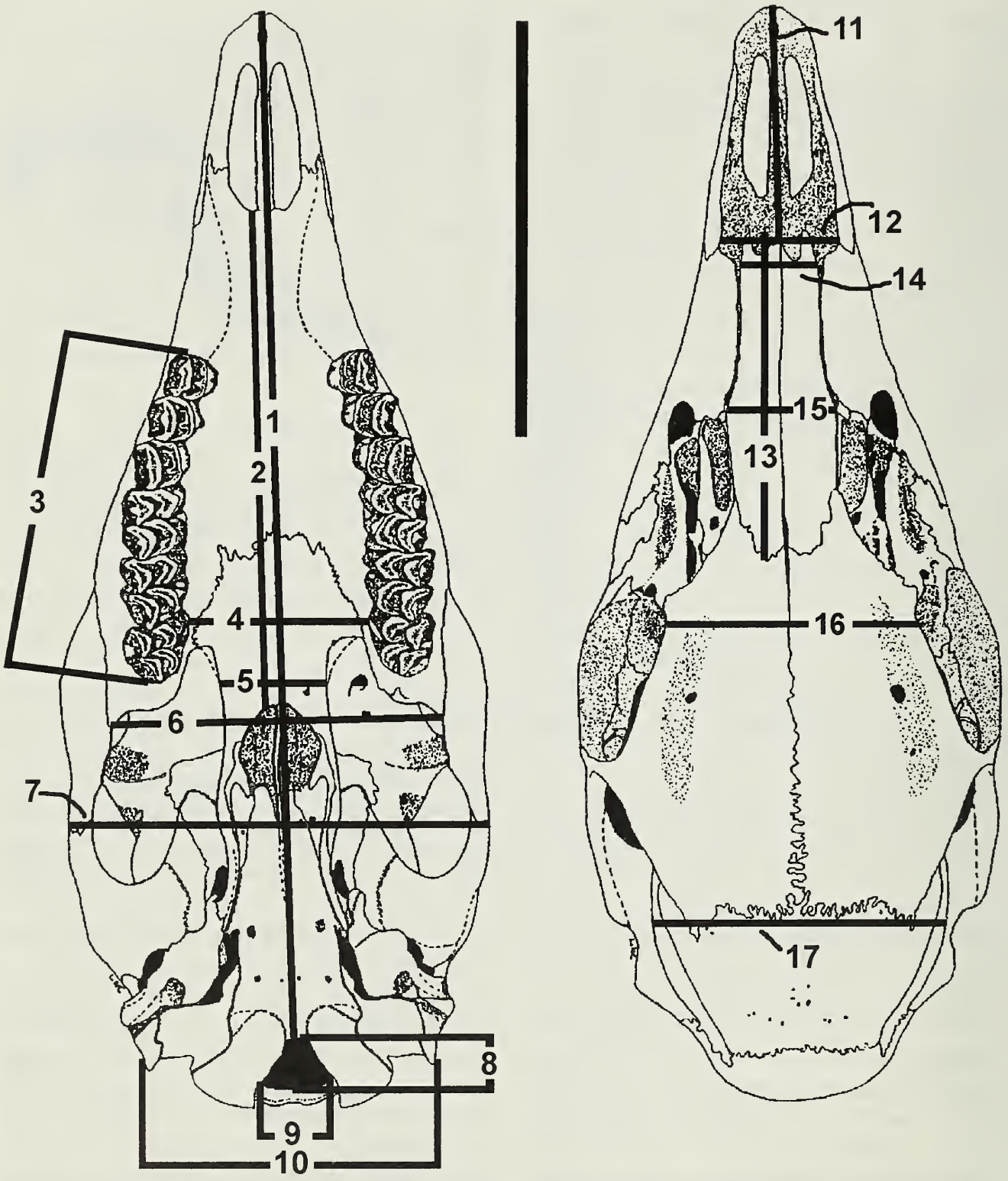

Fig. 2. Cranium of female white-tailed deer (*Odocoileus virginianus*; OSUFW [Oregon State University, Department of Fisheries and Wildlife mammal collection] 1140) illustrating dimensions recorded. 1, basilar length, 2, palatilar length, 3, length of upper molar series at alveolus, 4, breadth between M3s, 5, postpalatal breadth, 6, maxillary breadth, 7, zygomatic breadth, 8, height of foramen magnum, 9, width of foramen magnum, 10, mastoid breadth, 11, length of external nares, 12, breadth of external nares, 13, nasal length, 14, least nasal breadth, 15, greatest nasal breadth, 16, least interorbital breadth, and 17, breadth of braincase. The last dimension recorded was 18, depth of rostrum (not illustrated), which was measured with the cranium resting on a flat surface. It is the distance from the dorsal side of the premaxillae to the flat surface. Scale bar equals 10 cm.

year olds, and 3 contained ≥4 year olds. Males were sorted into four age classes for each collection area: age class 1 contained 2–2.9 year olds, 2 contained 3–3.9 year olds, 3 contained 4–5.9 year olds, and 4 contained ≥6 year olds.

Data were analyzed in SPSS 10.0.7 for Windows by use of the General Linear Model within a Multivariate Multiple Analysis of Variance (GLM MANOVA) and Canonical Discriminant Function Analysis (CDFA) with jackknife classification of specimens (Hair et al. 1987, McLachlan 1992). Age classes were designated as covariates because age was not a primary factor in acquiring specimens (Hair et al. 1987). Sample location (n = 3) and sex (n = 2) were treated as factors. Significance level was $P < 0.05$.

Initially, a GLM MANOVA was performed only with specimens having complete datasets (4 females and 2 males from Idaho, 14 females and 15 males from CWTDNWR, and 29 females and 10 males from Douglas Co., Oregon). The GLM MANOVA was repeated after data for each specimen were standardized by dividing each measurement by the area of its foramen magnum (A = 0.25π·width·height) to remove effects of size (Radinsky 1967) and to examine differences in shape of crania among collection areas. A CDFA was performed on standardized data present for the 11 dimensions deemed significant in the second GLM MANOVA for distinguishing specimens among the samples (6 females and 3 males from Idaho, 20 females and 22 males from CWTDNWR, and 38 females and 11 males from Douglas Co., Oregon) to present a pictorial representation of separation for specimens from the 3 localities.

Results

There was substantial variation among populations in cranial dimensions (Table 1). The initial GLM MANOVA of the original data indicated that significant differences (F = 3.673–123.501, df = 2) among specimens from the 3 sample areas occurred for all variables (Fig. 3A). When the interaction of collection area and sex was considered, however, only basilar length, least interorbital breadth, zygomatic breadth, and mastoid breadth were significantly different (f = 3.256–9.487, df = 2). The second GLM MANOVA of the standardized data set indicated significant differences (F = 3.772–13.911, df = 2) in the shape of the skulls for specimens among the three samples involving the following variables: basilar length, nasal length, breadth of the braincase, greatest width of nasals, least width of nasals, mastoid breadth, length of upper molar row, maxillary length, palatilar length, depth of rostrum, and width of external nares (Fig. 3B, Table 2). Values for these 11 standardized variables for specimens from the three samples were analyzed in CDFA (Fig. 4). The axis for Function 1 accounted for 71.4% of the variation in specimens among the areas and was related to skull shape. The axis for Function 2 incorporated the remaining variation (28.6%) in cranial dimensions, which was associated with overall skull size. All specimens from area 1, 85.7% of specimens from area 2, and 93.9% of specimens from area 3 were correctly classified into their *a priori* groups. Furthermore, in the plot of axes 1 and 2, with the exception of four individuals, three distinct groups were formed (Fig. 4). Even after controlling for differences in size related to sex and age, specimens from area 3 are distinguishable in the first axis from those in areas 1 and 2 by a combination of shorter basilar and nasal lengths, and narrower braincase and least width of the nasals (Table 1). On the second axis, specimens from area 1 are distinguishable from those in areas 2 and 3 by having longer basilar lengths and broader braincases. They also have narrower faces (as indicated by the narrower least width of the nasals) than specimens from area 2. Thus, it is apparent that even with size based on age and sex accounted for, specimens from area 3 (Douglas Co., Oregon) are still rel-

Table 1.—Means ± *SE*, ranges (in parentheses), and *CV*s followed by *n* of measurements of skull dimensions for female and male *Odocoileus virginanus* from northern Idaho, the Columbian White-tailed Deer National Wildlife Refuge (CWTDNWR) in Washington and Oregon, and Douglas Co., Oregon. Dimensions are shown in Fig. 2.

Dimensions	Northern Idaho		CWTDNWR		Douglas Co., Oregon	
	Males	Females	Males	Females	Males	Females
Basilar length	278.25 ± 3.010	251.17 ± 2.227	262.18 ± 1.490	244.57 ± 1.025	235.96 ± 1.592	223.74 ± 0.913
	(273–286)	(244–260)	(244–276)	(231–256)	(225–257)	(210–244)
	0.220, 4	0.022, 6	0.033, 33	0.025, 37	0.034, 25	0.034, 68
Palatilar length	135.62 ± 1.491	125.78 ± 1.991	125.74 ± 0.845	118.75 ± 0.591	113.69 ± 0.628	109.30 ± 0.620
	(130.8–139.6)	(120.2–131.6)	(114.3–140.0)	(109.3–127.5)	(104.8–122.4)	(97.9–123.1)
	0.027, 6	0.039, 6	0.045, 45	0.037, 54	0.045, 41	0.047, 68
Length of upper molar series	76.59 ± 1.167	74.53 ± 1.195	76.47 ± 0.359	73.89 ± 0.461	72.23 ± 0.465	70.09 ± 0.470
	(73.3–83.6)	(70.5–79.1)	(71.6–81.8)	(67.2–80.8)	(66.3–77.3)	(57.3–78.6)
	0.046, 9	0.039, 6	0.032, 47	0.044, 50	0.036, 31	0.052, 59
Breadth between M3s	49.61 ± 0.527	46.87 ± 0.685	46.99 ± 0.386	43.49 ± 0.279	45.62 ± 0.359	42.85 ± 0.284
	(47.4–53.5)	(45.1–49.1)	(42.7–54.9)	(39.7–49.3)	(39.7–52.8)	(36.2–47.6)
	0.035, 11	0.036, 6	0.054, 44	0.050, 60	0.052, 44	0.055, 70
Postpalatal breadth	28.95 ± 0.384	26.52 ± 0.694	25.89 ± 0.158	24.76 ± 0.218	24.88 ± 0.242	24.13 ± 0.223
	(26.4–30.4)	(24.8–28.4)	(22.6–30.7)	(20.3–30.7)	(21.4–29.3)	(20.9–27.8)
	0.042, 10	0.059, 5	0.060, 48	0.065, 55	0.062, 41	0.073, 62
Maxillary breadth	86.54 ± 1.406	82.38 ± 1.002	82.89 ± 0.515	78.46 ± 0.362	81.91 ± 0.492	79.13 ± 0.377
	(79.7–93.2)	(78.5–85.5)	(75.8–91.2)	(72.7–87.6)	(73.9–88.0)	(70.3–86.4)
	0.054, 11	0.030, 6	0.043, 47	0.037, 64	0.040, 44	0.042, 77
Zygomatic breadth	116.69 ± 1.152	108.28 ± 1.274	108.73 ± 0.788	101.37 ± 0.358	105.67 ± 0.460	100.87 ± 0.514
	(113.0–124.5)	(104.9–113.0)	(96.5–120.0)	(95.9–107.3)	(99.9–111.4)	(90.40–116.4)
	0.033, 11	0.029, 6	0.049, 45	0.028, 62	0.029, 43	0.044, 74
Height of foramen magnum	20.67 ± 0.439	21.83 ± 0.381	18.96 ± 0.180	19.97 ± 0.176	19.56 ± 0.197	20.19 ± 0.022
	(18.0–23.2)	(20.7–23.1)	(14.4–21.8)	(16.9–23.6)	(16.7–22.7)	(17.4–23.9)
	0.074, 12	0.043, 6	0.068, 51	0.071, 64	0.071, 49	0.065, 77
Width of foramen magnum	20.36 ± 0.539	20.83 ± 0.305	19.29 ± 0.182	19.49 ± 0.134	19.67 ± 0.196	18.94 ± 0.136
	(16.2–22.0)	(19.9–22.1)	(16.5–22.4)	(17.1–22.2)	(17.0–22.2)	(16.3–22.5)
	0.092, 12	0.036, 6	0.067, 50	0.055, 64	0.070, 49	0.063, 77
Mastoid breadth	86.63 ± 1.154	73.03 ± 1.403	75.19 ± 0.744	65.46 ± 0.311	69.28 ± 0.531	62.47 ± 0.376
	(82.3–96.5)	(68.3–76.9)	(64.5–90.6)	(59.7–71.5)	(62.3–79.7)	(54.4–69.0)
	0.046, 12	0.047, 6	0.070, 50	0.038, 64	0.054, 49	0.053, 78
Length of external nares	78.28 ± 1.372	70.70 ± 1.343	73.44 ± 0.658	69.81 ± 0.560	70.76 ± 0.841	67.01 ± 0.492
	(74.3–80.6)	(67.6–76.7)	(62.3–80.3)	(63.8–77.6)	(63.4–80.0)	(53.6–76.5)
	0.035, 4	0.047, 6	0.052, 33	0.047, 35	0.059, 25	0.061, 69

Table 1.—Continued.

Dimensions	Northern Idaho		CWTDNWR		Douglas Co., Oregon	
	Males	Females	Males	Females	Males	Females
Breadth of external nares	33.88 ± 0.892	29.67 ± 0.966	31.87 ± 0.390	30.58 ± 0.426	28.59 ± 0.406	27.73 ± 0.291
	(31.8–35.6)	(26.5–33.2)	(27.4–34.9)	(23.7–34.5)	(23.9–33.1)	(22.7–34.4)
	0.053, 4	0.080, 6	0.064, 27	0.080, 33	0.063, 20	0.086, 67
Nasal length	89.60 ± 2.486	83.12 ± 0.908	83.18 ± 0.788	76.35 ± 0.717	69.15 ± 0.917	65.80 ± 0.578
	(81.6–100.4)	(80.9–86.8)	(70.4–95.0)	(62.7–88.9)	(52.6–79.1)	(50.5–79.3)
	0.073, 7	0.027, 6	0.062, 43	0.066, 50	0.088, 44	0.078, 78
Least nasal breadth	20.05 ± 0.757	17.25 ± 0.575	21.41 ± 0.339	19.00 ± 0.212	18.85 ± 0.222	17.34 ± 0.205
	(17.4–23.9)	(15.6–19.3)	(16.8–25.9)	(16.0–22.9)	(16.8–22.5)	(13.5–20.8)
	0.107, 8	0.082, 6	0.103, 42	0.077, 48	0.073, 38	0.098, 68
Greatest nasal breadth	30.32 ± 0.934	24.95 ± 0.768	29.23 ± 0.395	26.53 ± 0.325	26.14 ± 0.125	24.38 ± 0.285
	(24.5–33.1)	(22.3–27.5)	(24.6–37.0)	(23.2–32.7)	(22.4–31.0)	(18.7–33.2)
	0.092, 9	0.075, 6	0.087, 42	0.085, 48	0.083, 38	0.098, 70
Least interorbital breadth	71.58 ± 0.754	61.53 ± 0.580	63.07 ± 0.499	58.10 ± 0.308	60.65 ± 0.395	56.21 ± 0.313
	(68.0–77.2)	(60.1–63.3)	(54.9–73.8)	(50.9–63.6)	(55.8–67.3)	(50.5–62.5)
	0.037, 12	0.023, 6	0.056, 50	0.043, 65	0.046, 49	0.050, 80
Breadth of braincase	79.20 ± 1.268	71.33 ± 0.516	74.00 ± 0.480	71.23 ± 0.304	72.39 ± 0.357	69.35 ± 0.250
	(71.2–85.1)	(69.0–72.7)	(61.5–80.6)	(66.7–76.8)	(67.4–76.8)	(36.2–47.6)
	0.055, 12	0.018, 6	0.047, 52	0.034, 65	0.034, 48	0.055, 70
Elevation of rostrum	32.53 ± 2.199	31.27 ± 1.619	38.98 ± 0.991	38.83 ± 0.929	36.21 ± 1.236	33.89 ± 0.732
	(27.3–37.8)	(25.7–35.0)	(25.6–46.4)	(24.9–49.5)	(27.0–51.2)	(17.2–47.0)
	0.135, 4	0.127, 6	0.134, 28	0.142, 35	0.164, 23	0.171, 63

Table 2.—Covariate and factors affecting 16 standardized response variables recorded from skulls of *Odocoileus virginianus* from the CWTDNWR, Washington and Oregon, Douglas Co., Oregon, and northern Idaho. We standardized data for response variables by dividing each measurement by the area of the foramen magnum ($A = 0.25\pi WH$) for that individual (Radinsky 1967). The General Linear Model is presented for each statistically significant response variable as SS, MS with f and p below except for the Error column. The covariate Age class had 3 classes for females and 4 for males. The factors were sex (female, male) and collection locality.

Response variables and multivariate test	Age class *d.f.* = 1	Sex *d.f.* = 1	Collection locality *d.f.* = 2	Collection locality + Sex *d.f.* = 2	Corrected model *d.f.* = 6	Error *d.f.* = 67
Basilar length		0.053, 0.053	0.079, 0.039		0.244, 0.041	0.467,
		7.64, 0.007	5.66, 0.005		5.84, 0.0001	0.007
Nasal length		0.005, 0.005	0.025, 0.012		0.0440, 0.007	0.066,
		4.68, 0.034	12.56, 0.0001		7.45, 0.0001	0.001
Greatest nasal breadth		0.001, 0.001	0.002, 0.001		0.005, 0.0001	0.013,
		7.00, 0.010	4.21, 0.019		4.54, 0.001	0.0001
Least nasal breadth	0.0003, 0.0003	0.001, 0.001	0.001, 0.001		0.003, 0.0001	0.005,
	4.34, 0.041	9.70, 0.003	6.26, 0.003		7.20, 0.0001	0.00001
Least interorbital breadth		0.007, 0.007			0.014, 0.002	0.034,
		12.74, 0.001			4.40, 0.001	0.0001
Zygomatic breadth		0.009, 0.009			0.026, 0.004	0.095,
		6.68, 0.012			3.09, 0.010	0.001
Breadth of braincase		0.003, 0.003	0.005, 0.002		0.015, 0.002	0.043,
		4.17, 0.045	3.67, 0.031		3.80, 0.003	0.001
Mastoid breadth		0.017, 0.017	0.003, 0.002	0.005, 0.003	0.039, 0.006	0.032,
		34.61, 0.0001	3.14, 0.050	5.10, 0.009	13.32, 0.0001	0.001
Length of upper molar			0.008, 0.004		0.013, 0.002	0.044,
series at alveolus			6.01, 0.004		3.29, 0.007	0.001
Maxillary breadth					0.013, 0.002	0.058,
					2.49, 0.031	0.001
Breadth between M3s					0.005, 0.001	0.022,
					2.57, 0.027	0.001
Palatilar length		0.009, 0.009	0.018, 0.009		0.051, 0.008	0.121,
		4.84, 0.031	4.91, 0.010		4.72, 0.0001	0.002
Postpalatal breadth		0.0001, 0.0001			0.001, 0.0002	0.007,
		4.04, 0.049			2.17, 0.057	0.0001
Elevation of rostrum			0.006, 0.003		0.010, 0.002	0.035,
			5.69, 0.005		3.31, 0.006	0.001
Length of external nares		0.003, 0.003			0.012, 0.002	0.038,
		6.01, 0.017			3.65, 0.003	0.001

Table 2.—Continued.

Response variables and multivariate test	Age class $d.f. = 1$	Sex $d.f. = 1$	Collection locality $d.f. = 2$	Collection locality + Sex $d.f. = 2$	Corrected model $d.f. = 6$	Error $d.f. = 67$
Breadth of external nares			0.001, 0.001		0.003, 0.001	0.009,
			5.16, 0.008		3.71, 0.003	0.001
Wilkes' Lambda	Value = 0.550	Value = 0.269	Value = 0.088	Value = 0.449		
	$f = 2.65$	$f = 8.82$	$f = 7.74$	$f = 1.60$		
	$d.f. = 16$,	$d.f. = 16$,	$d.f. = 32$,	$d.f. = 32$,		
	$p = 0.004$	$p = 0.0001$	$p = 0.0001$	$p = 0.040$		

atively smaller animals with shorter faces and narrower skulls than those specimens from either area 1 (northern Idaho) or area 2 (CWTDNWR).

Discussion

Assumptions and limitations of analyses.—Although we collected a reasonably large number of skulls from each of the localities, incomplete data from many specimens substantially reduced our sample sizes for statistical analysis, especially specimens assigned to *O. v. ochrourus*. Small sample size can be problematic, especially for MANOVA where statistical power is easily compromised (Johnson & Wichern 1998). In addition, departure from normality, an important assumption of MANOVA, occurs more frequently with small sample sizes. Fortunately, MANOVA is relatively robust to violations of assumptions in many circumstances (Johnson & Wichern 1998). Also, because of the large effect size (differences among means of treatments) among populations with many cranial dimensions, statistical power probably was not an issue in our analyses. Comparisonwise error rates ranged from 0.013 to 0.0001 (Table 2).

Small sample size also contributes to classification bias in CDFA, a consequence of which is an overestimate of divergence among taxa (Lance et al. 2000). In this study, we used the results of CDFA strictly for illustrative rather than analytical purposes. Still, we used a less biased jackknife technique for subsequent classification of specimens (Hair et al. 1987, McLachlan 1992, Johnson & Wichern 1998, Lance et al. 2000).

Cranial variation and taxonomy.—The taxonomy of white-tailed deer, like that of most of the North American mammal fauna, predates development of genetic techniques and consequently early descriptions of taxa were based on variation of morphological attributes, especially cranial characteristics (e.g., *Ovis canadensis*, Cowan

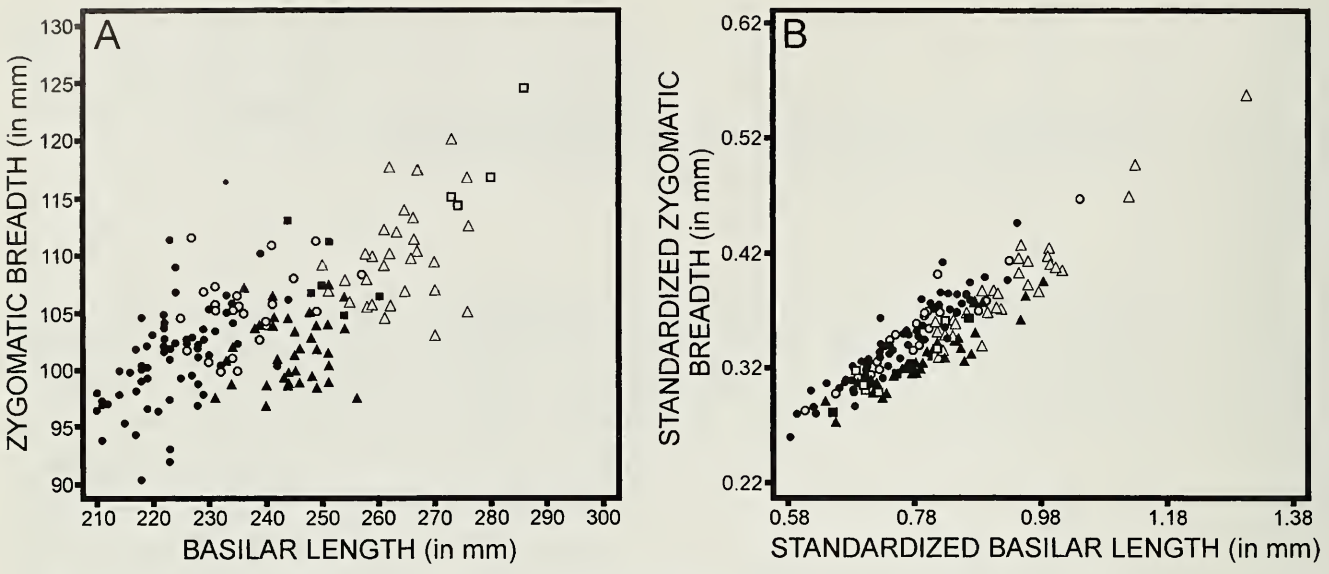

Fig. 3. A. Plot of basilar length and zygomatic breadth illustrating a decrease in size of female and male white-tailed deer (*Odocoileus virginianus*) from northern Idaho (females ■, males □), the Columbian White-tailed Deer National Wildlife Refuge in Washington and Oregon (females ▲, males △), to Douglas Co., Oregon (females ●, males ○). B. Plot of standardized basilar length and standardized zygomatic breadth illustrating the same relative sizes for female and male white-tailed deer (*Odocoileus virginianus*) from the same collection areas.

1940). Much of the historical taxonomy of species and subspecies lacks an adequate quantitative basis and reflects a typological view inconsistent with an evolutionary perspective (Ball & Avise 1992, Wehausen & Ramey 2000). Recent developments in molecular biology (e.g., Cook et al. 2001) and statistical analyses (e.g., Steppan & Sullivan 2000) have changed the way mammalogists do systematics, which in many instances has resulted in revisions of existing taxonomy (Steppan & Sullivan 2000, Wehausen & Ramey 2000, Cook et al. 2001). Still, morphometry can be a useful tool in elucidating evolutionary and taxonomic relationships (Wehausen & Ramey 1993, Genov 1999, Molina & Molinari 1999), especially when used in conjunction with genetic data (e.g., Wehausen & Ramey 2000).

We used variation in cranial morphology to test the hypothesis that deer in the three populations belong to a single taxon. This hypothesis was proposed on the basis of allozyme variation among three white-tailed deer populations (Gavin & May 1988). The results of our analyses indicate significant variation among the three populations for several cranial dimensions (Table 2). Thus, our results do not support the current taxonomy, which implies that white-tailed deer from the lower Columbia River and Douglas Co. (*O. v. leucurus*) are similar, yet distinguishable from white-tailed deer in eastern Oregon, eastern Washington, and Idaho (*O. v. ochrourus*). Rather, our results clearly delineate three distinct morphological populations (Fig. 4, Table 2) rather than a single unified taxon.

Similar geographical variation in cranial dimensions has been reported for bighorn sheep, *Ovis canadensis* Shaw (Wehausen & Ramey 1993, 2000), wild boar, *Sus scrofa* Linnaeus (Genov 1999), black bear, *Ursus americanus* Pallas (Kennedy et al. 2002), and other white-tailed deer (Molina & Molinari 1999). The key issue in interpreting cranial variation in the context of subspecific taxonomy is whether the morphological variation is indicative of corresponding genetic divergences; or, whether it is largely ecophenotypic variation that resulted from regional differences in habitat or other environmental differences (Wehausen & Ramey 2000, Kennedy et al. 2002). Some taxa (e.g., black bear) show clinal variation, i.e., significant correlations between skull mor-

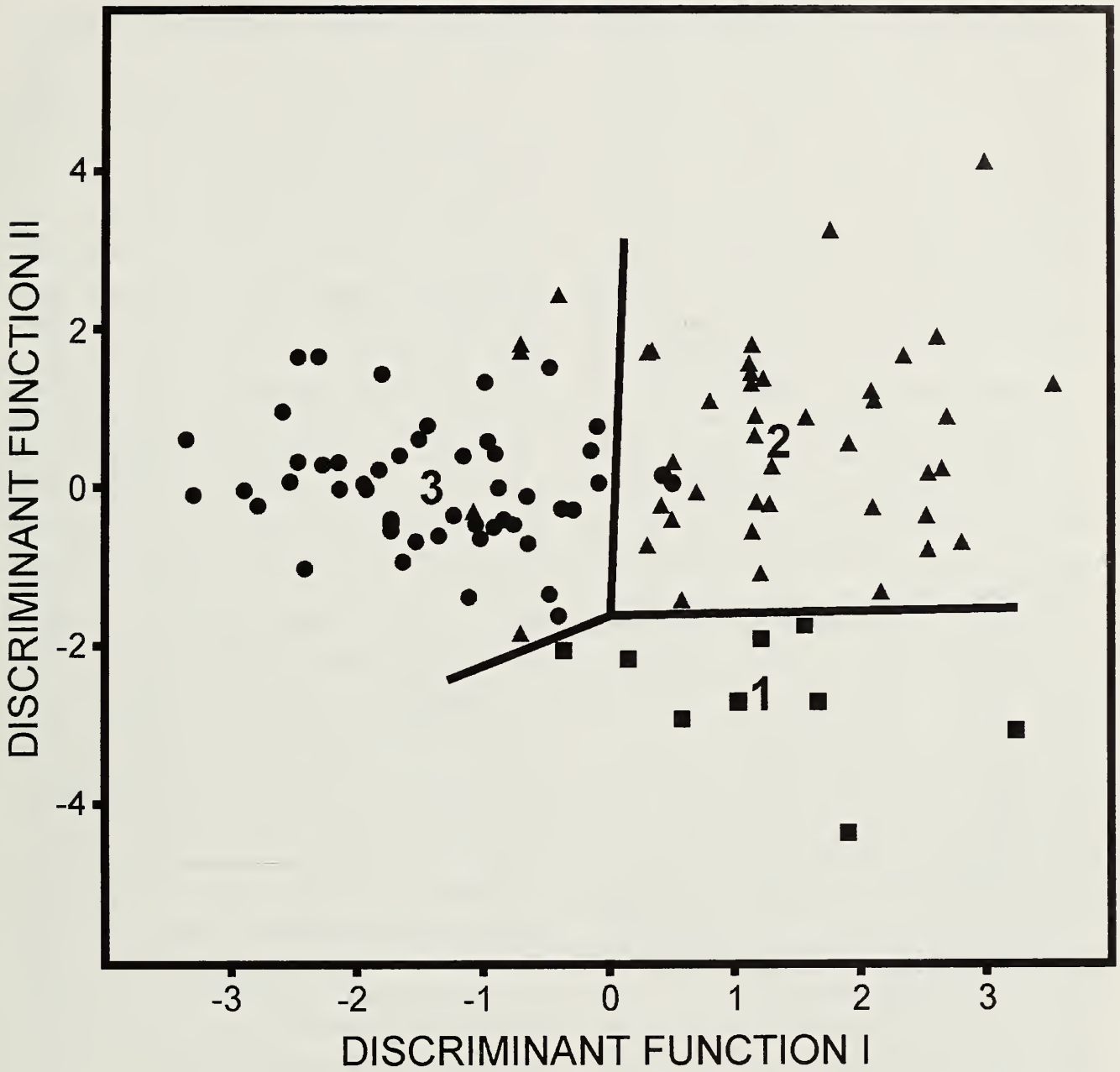

Fig. 4. Canonical-variates plot of specimens from 1 (■), northern Idaho, 2 (▲), the Columbian White-tailed Deer National Wildlife Refuge in Washington and Oregon, and 3 (●), Douglas Co., Oregon. Function 1 accounted for 71.4% and Function 2 28.6% of the variation among the areas. Group centroids are indicated by numbers. Specimens from the three areas sorted into three distinct morphological groups; straight lines, drawn by eye, within the graph delineate the groups. Differences in shape of the cranium are characterized as follows: specimens from area 3 have overall shorter and narrower skulls than those from areas 1 and 2; and specimens from area 1 have a longer rostrum (as indicated by significantly longer nasals) and narrower cranium than those from area 2.

phology and climatic or other environmental gradients (Kennedy et al. 2002), and display substantial genetic dissimilarity among regional populations (Miller 1995). In our study, the pattern of cranial variation was somewhat similar to that reported for black bears (Kennedy et al. 2002) with skull size varying along a west to east gradient and decreasing from north to south. The lower Columbia River population had features intermediate between those of the Idaho and Douglas Co. populations. Unlike black bears (Miller 1995), however, there was no clear evidence of corresponding genetic divergences at one locus among the disjunct regional populations (Gavin & May 1988).

Gavin & May (1988) reported that white-tailed deer populations from the Pacific Northwest showed relatively low genetic divergence. In a large number of possible pair-wise comparisons Gavin & May (1988) found Nei's (1971) genetic distances between *O. v. borealis* from New York and white-tailed deer populations from the Pacific Northwest (0.037) were an order of magnitude greater than genetic differences among white-tailed deer populations of Oregon and Washington. Moreover, white-tailed deer from Idaho showed less divergence from the Douglas Co. population than from the lower Columbia River population. Genetic distances (Nei 1971) between *O. v. ochrourus* from Oregon and Washington and *O. v. leucurus* in southwestern Oregon, and between *O. v. ochrourus* and white-tailed deer from the lower Columbia River were 0.003 and 0.010, respectively. Also, they found that genetic divergence between *O. v. leucurus* populations on the Oregon and Washington sides of the lower Columbia River (0.007) was greater than between sampled *O. v. ochrourus* populations in Oregon and Washington (Fig. 1), or between *O. v. leucurus* populations in southwestern Oregon and *O. v. ochrourus* populations (0.002).

Genetic and morphological data commonly suggest different conclusions regarding taxonomy of mammals. Recent examples include *Ovis canadensis* (Wehausen & Ramey 1993, 2000) and *Sus scrofa* (Genov 1999), where separation of subspecies based solely on morphology (Cowan 1940, Genov 1999) was not supported by more rigorous analysis in conjunction with genetic data (Wehausen & Ramey 2000). The tendency has been to rely on molecular data, which presumably provides less ambiguous evidence. Ball & Avise (1992) proposed that subspecies are major subdivisions of the gene pool diversity of species where such subunits can be corroborated by independent, genetically based traits. According to this view, subspecies should have distinguishing attributes that have an evolutionary basis (Wehausen & Ramey 2000).

We found white-tailed deer populations of Oregon and Washington distinguishable by cranial dimensions, but Gavin & May (1988) found no compelling evidence from an evolutionary basis for this variation. The putative historical ranges of *O. virginianus* populations in the Pacific Northwest (Bailey 1932, Grinnell 1933, Smith 1985, Williams 1986, Gavin & May 1988) suggest that populations interbred freely. Before European settlement, white-tailed deer occupied most of the riparian floodplains and other deciduous lowlands in western, central, and northeastern Oregon. The range of *O. v. ochrourus* extended from northeastern California (Grinnell 1933) north to west-central British Columbia and east to north-central Wyoming (Hall 1981, Smith 1991). In Oregon, *O. v. ochrourus* occurred in the Klamath Basin (Walsingham 1873), which is only about 100 km east of the southernmost range of *O. v. leucurus* in southwestern Oregon (Smith 1985). Throughout east-central Oregon, *O. v. ochrourus* occupied floodplain and riparian communities, frequenting deciduous woodlands and woody thickets associated with streams and marshes (Walsingham 1873, Cowan 1936). Similarly, *O. v. leucurus* occurred throughout the river valleys and other deciduous woodlands of western Oregon (Smith 1985). The Cascade Range likely represented a barrier for free movement of white-tailed deer between central and western Oregon; however, opportunities for gene flow before European settlement presumably existed along the Columbia River and in south-central Oregon where river valleys cut through the Cascade Range at relatively low elevations. Without geographic isolation or strong selective pressures associated with markedly different environmental conditions (e.g., Wehausen & Ramey 1993, 2000), there is little reason to believe that historic populations of white-tailed deer in Oregon (and the Pacific Northwest) were not a single, contiguous breeding population.

Today, circumstances are very different; the populations clearly are isolated from one another (Fig. 1). White-tailed deer in northeastern Oregon apparently have extended their range westward and southward in recent years (Oregon Department of Fish and Wildlife, unpubl. data). Still, land use and natural barriers throughout central Oregon represent significant impediments to dispersal and natural expansion. Efforts to translocate deer may establish isolated local populations, but much of the native habitat in central Oregon has been modified (Verts & Carraway 1998). Moreover, availability and connectivity of habitat in western Oregon and along the Columbia River is such that future opportunities for natural or facilitated expansion are unlikely. This, combined with the potential competition from black-tailed deer *Odocoileus hemionus* (Smith 1985), renders the likelihood of *O. v. leucurus* reoccupying significant portions of its historic range extremely low.

We believe it is prudent to consider the question of taxonomy in the context of current circumstances rather than belabor what might have been. Neither earlier genetic research nor our morphological study provides compelling evidence to warrant an unambiguous resolution of this question. Consequently, the current taxonomy, although not directly supported by either line of evidence, cannot be refuted with certainty. Nonetheless, the three populations are morphologically distinct, geographically isolated, occupy different habitats (Gavin 1979, Smith 1985, Verts & Carraway 1998), and likely represent unique genepool subdivisions of *O. virginianus* (Ball & Avise 1992, Wehausen & Ramey 2000). With these populations isolated and gene flow interrupted, genetic divergence may become significant in time (Avise 1994).

Implications for recovery and conservation.—Nomenclature shapes the view of how nature is organized (Avise 1994) and taxonomic units have become the foundation of conservation efforts (Cook & MacDonald 2001). Current taxonomy views white-tailed deer populations of the lower Columbia River and Douglas Co. as *O. v. leucurus,* which may allow translocation of individuals from either location for the purpose of restoring populations in portions of its historic range. Our results do not support current taxonomy, but indicate that deer from the lower Columbia River and Douglas Co. are morphologically distinct. Because of geographic isolation and differences in habitat, we believe that in time the two populations will become sufficiently genetically divergent to warrant separation into two taxa. For that reason, we think it is prudent to choose a conservative approach to restoring white-tailed deer in western Oregon and refrain from translocating deer from Douglas Co. (or eastern Oregon) to supplement populations along the lower Columbia River or establish populations in the Willamette River valley.

Acknowledgments

We thank curators and collection managers at the American Museum of Natural History, Mammal Division, the University of Puget Sound, James R. Slater Museum of Natural History, and the University of Idaho, Bird and Mammal Museum for loan of or access to specimens in their care. N. Slade, Natural History Museum, University of Kansas and P. Sullivan, Department of Natural Resources, Cornell University, provided statistical assistance. B. Albritton Coblentz assisted WPS with sectioning and staining of tooth sections. Portions of this research were supported by a grant from the U.S. Fish and Wildlife Service to WPS and LNC. A. Gardner, M. Kennedy, and J. Wehausen provided valuable comments on an earlier draft that improved the quality of this paper.

Literature Cited

Avise, J. 1994. Molecular markers, natural history, and evolution. Chapman and Hall, New York, 511 pp.

Bailey, V. 1932. The northwestern white-tail deer.—

Proceedings of the Biological Society of Washington 45:43–44.

———. 1936. The mammals and life zones of Oregon.—North American Fauna 55:1–416.

Ball, M. R., & J. C. Avise. 1992. Mitochondrial DNA phylogeographic differentiation among avian populations and the significance of subspecies.—The Auk 109:626–636.

Columbian White-tailed Deer Recovery Team. 1983. Revised Columbian white-tailed deer recovery plan. U.S. Fish and Wildlife Service, Portland, Oregon, 75 pp.

Cook, J. A., & S. O. MacDonald. 2001. Should endemism be a focus of conservation efforts along the north Pacific coast of North America?—Biological Conservation 97:207–213.

———, A. L. Bidlack, C. J. Conroy, J. R. Demboski, M. A. Fleming, A. M. Runck, K. D. Stone, & S. O. MacDonald. 2001. A phylogeographic perspective on endemism in the Alexander Archipelago of southeast Alaska.—Biological Conservation 97:215–227.

Cowan, I. M. 1936. Distribution and variation in deer (*Odocoileus*) of the Pacific Coastal Region of North America.—California Fish and Game 22: 155–246.

———. 1940. Distribution and variation in the native sheep of North America.—The American Midland Naturalist 24:505–580.

Crews, A. K. 1939. A study of the Oregon white-tailed deer, *Odocoileus virginianus leucurus* (Douglas). M.S. thesis, Oregon State University, Corvallis, 45 pp.

Doremus, H., & J. E. Pagel. 2001. Why listing may be forever: perspectives on delisting under the U.S. Endangered Species Act.—Conservation Biology 15:1258–1268.

Douglas, D. 1829. Observations on two undescribed species of North American mammals (*Cervus leucurus* et *Ovis californicus*).—Zoological Journal 4:330–332.

———. 1914. Journal kept by David Douglas during his travels in North America 1823–1827. W. Wesley and Son, London, U.K., 364 pp.

Dublin, H. T. 1980. Relating deer diets to forage quality and quantity—the Columbian white-tailed deer. M.S. thesis, University of Washington, Seattle, 135 pp.

Gavin, T. A. 1979. Population ecology of the Columbian white-tailed deer. Ph.D. dissertation, Oregon State University, Corvallis, 149 pp.

———, & B. May. 1988. Taxonomic status and genetic purity of Columbian white-tailed deer.—The Journal of Wildlife Management 52:1–10.

———, L. H. Suring, P. A. Vohs, Jr., & E. C. Meslow. 1984. Population characteristics, spatial organization, and natural mortality in the Columbian white-tailed deer.—Wildlife Monographs 91:1–41.

Gee, K. L., J. H. Holman, M. K. Causey, A. N. Rossi, & J. B. Armstrong. 2002. Aging white-tailed deer by tooth replacement and wear: a critical evaluation of a time-honored technique.—Wildlife Society Bulletin 30:387–393.

Genov, P. V. 1999. A review of the cranial characteristics of the wild boar (*Sus scrofa* Linnaeus 1758), with systematic conclusions.—Mammal Review 29:205–238.

Grinnell, J. 1933. Review of the Recent mammal fauna of California.—University of California Publications in Zoology 40:71–284.

Hair, J. F., Jr., R. E. Anderson, & R. L. Tatham. 1987. Multivariate data analysis with readings, 2nd edition. Macmillan Publishing Company, New York, 449 pp.

Hall, E. R. 1981. The mammals of North America. Wiley-Interscience, New York, 2:601–1181 + *90.*

Jewett, S. G. 1914. The white-tailed and other deer in Oregon.—The Oregon Sportsman 2:5–9.

Johnson, R. A., & D. W. Wichern. 1998. Applied multivariate statistical analysis, 4th edition. Prentice-Hall, Upper Saddle River, New Jersey, 816 pp.

Kennedy, M. L., P. K. Kennedy, M. A. Bogan, & J. L. Waits. 2002. Geographic variation in the black bear (*Ursus americanus*) in the eastern United States and Canada.—Southwestern Naturalist 47:257–266.

Lance, R. E., M. L. Kennedy, & P. L. Leberg. 2000. Classification bias in discriminant function analysis used to evaluate putatively different taxa.—Journal of Mammalogy 81:245–249

Larson, J. S., & R. D. Taber. 1980. Criteria of sex and age. Pp. 143–202 *in* S. D. Schemnitz, ed., Wildlife management techniques manual, 4th edition, The Wildlife Society, Washington, D.C., 686 pp.

McLachlan, G. J. 1992. Discriminant analysis and statistical pattern recognition. John Wiley & Sons, Inc., New York, 526 pp.

Miller, D. A. 1995. Systematic classification of black bears in the southeastern United States. M.S. thesis, Virginia Tech University, Blacksburg, 102 pp.

Molina, M., & J. Molinari. 1999. Taxonomy of Venezuelan white-tailed deer (*Odocoileus,* Cervidae, Mammalia) based on cranial and mandibular traits.—Canadian Journal of Zoology 77: 632–645.

Nei, M. 1971. Identity of genes and genetic distance between populations.—Genetics 68(Supplement):47.

Radinsky, L. 1967. Relative brain size: a new measure.—Science 155:836–837.

Ricca, M. A. 2000. Movements, habitat associations, and survival of Columbian white-tailed deer in Western Oregon. M.S. thesis, Oregon State University, Corvallis, 170 pp.

Scheffer, V. B. 1950. Growth layers on the teeth of Pinnipedia as an indication of age.—Science 112:309–311.

Severinghaus, C. W. 1949. Tooth development and wear as criteria of age in white-tailed deer.—Journal of Wildlife Management 13:195–216.

Smith, W. P. 1982. Status and habitat use of Columbian white-tailed deer in Douglas County, Oregon. Ph.D. dissertation, Oregon State University, Corvallis, 273 pp.

———. 1985. Current geographic distribution and abundance of Columbian white-tailed deer, *Odocoileus virginianus leucurus* (Douglas).—Northwest Science 59:243–251.

———. 1987. Dispersion and habitat use by sympatric Columbian white-tailed deer and Columbian black-tailed deer.—Journal of Mammalogy 68: 337–347.

———. 1991. Odocoileus virginianus.—Mammalian Species 388:1–13.

Steppan, S. J., & J. Sullivan. 2000. The emerging statistical perspective in systematics: a comment on Mares and Braun.—Journal of Mammalogy 81:260–270.

Suring, L. H., & P. A. Vohs, Jr. 1979. Habitat use by Columbian white-tailed deer.—Journal of Wildlife Management 43:610–619.

Verts, B. J., & L. N. Carraway. 1998. Land mammals of Oregon. University of California Press, Berkeley, 668 pp.

Wehausen, J. D., & R. R. Ramey. 1993. A morphometric reevaluation of the Peninsular subspecies.—Desert Bighorn Council Transactions 37: 1–10.

———, & R. R. Ramey, II. 2000. Cranial morphometric and evolutionary relationships in the northern range of *Ovis canadensis*.—Journal of Mammalogy 81:145–161.

Walsingham, T. L. 1873. On the distribution of the different species of deer and other ruminants in northern California and Oregon.—Proceedings of the Zoological Society of London 1873:561–563.

Whitney, L. W. 2001. Ecological relationships between Columbian white-tailed and black-tailed deer in Southwest Oregon. M.S. thesis, Oregon State University, Corvallis, 106 pp.

Williams, D. F. 1986. Mammalian species of special concern in California. Wildlife Management Division Administrative Report 86-1, California Department of Fish and Game, Sacramento, 111 pp.